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FIELDIANA

Geology

Published by Field Museum of Natural History

Volume 20, No. 6

January 25, 1971

A Strange Arthropod from the Mazon Creek of Illinois and the Trans Permo-Triassic Merostomoidea (Trilobitoidea)

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An arthropod from the ironstone concretions of the Middle Pennsylvanian Essex fauna of Illinois (Johnson and Richardson, 1966) appears to be closely related to two Mesozoic species, *Euthycarcinus kessleri* Handlirsch, 1914, from the Lower Triassic of Germany, and *Synaustus brookvalensis* Riek, 1964, from the Middle Triassic of Australia. Together these animals appear to constitute the latest known occurrence of trilobitoids in the fossil record.

Specimens of various collections have been used in this study and are denoted by prefixes as follows:

PE—Field Museum of Natural History

H—Collection of Mr. Jerry Herdina, Berwyn, Illinois

S—Collection of Mr. and Mrs. Levi Sherman, Des Plaines, Illinois

T—Collection of Mr. Francis Tully, Lockport, Illinois

HTP—Collection of Mr. and Mrs. Ted Piecko, Chicago, Illinois.

DESCRIPTION

Trilobitomorpha Størmer, 1944

Trilobitoidea Størmer, 1959

Merostomoidea Størmer, 1944

Euthycarcinoidea Gall and Grauvogel, 1964
(*emend.* Schram, herein)

Library of Congress Catalog Card Number: 73-143279

Publication 1119

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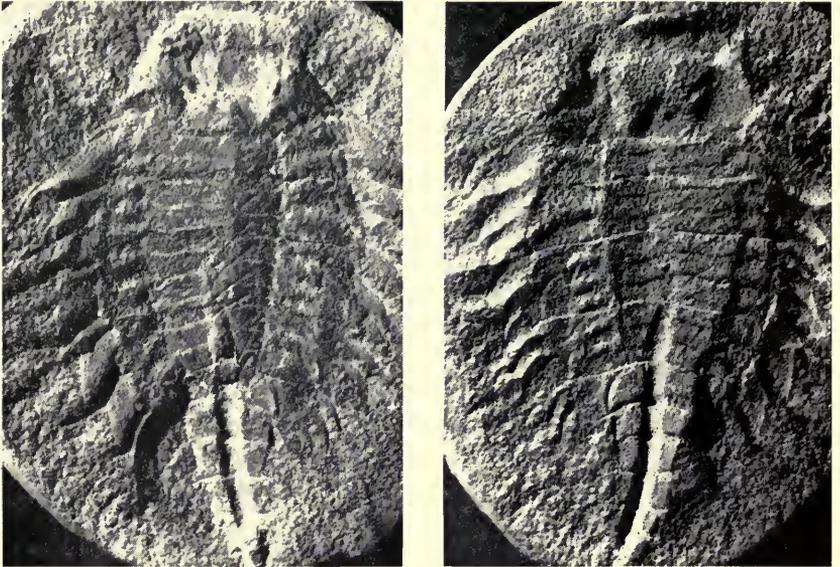


FIG. 1. *Kottixerxes gloriosus*. T3, note relationship of sternites to the large preabdominal plates and the outlines of the preabdominal appendages bearing setae. $\times 1.8$.

Merostomoidea with elongate body divided into three distinct body regions: a head with sessile eyes, a pre-abdomen with tergites fused in groups and with well-developed rod-like "ligaments," and a post-abdomen; a styloid telson; the appendages of the typical trilobitoid type. *M. Penn.*—*M. Trias*.

Euthycarcinidae Handlirsch, 1914

Head consisting of acron plus four (?) segments; preabdomen of 11 or 12 segments ventrally, with tergites fused to form five elements dorsally; four or five postabdominal somites.

Kottixerxes n. gen.

Diagnosis.—Euthycarcinid of moderate size; preabdominal tergites fused into plates, with the numbers of segments associated in these plates being two, two, three, three, one respectively from anterior to posterior; eyes sessile, ovoid in shape; five segments in the postabdomen, each tapering posteriorly; a relatively short telson.

Type species.—*Kottixerxes gloriosus* Schram, n. sp.



FIG. 2. *Kottixerxes gloriosus*. H406. $\times 3.5$.

***Kottixerxes gloriosus* n. sp.** Figures 1-9.

Description.—The cephalon is bluntly rounded in outline anteriorly, with slightly developed “genal” spines (T3, fig. 1). The entire surface texture of the head shield is rough and somewhat papillose (T3). The sessile ovoid eyes are located on the edge of the cephalon at the anterolateral corners, H406 (fig. 2), which displays these as very faint, ghostly outlines. H122 (fig. 3) has what appear to be segments in the cephalic area. Whether these segments belong to the cephalon or are actually sternites of the anterior preabdomen cannot be determined.

The five dorsal plates of the preabdomen are formed by the fusion of the preabdominal tergites. The first two plates are com-

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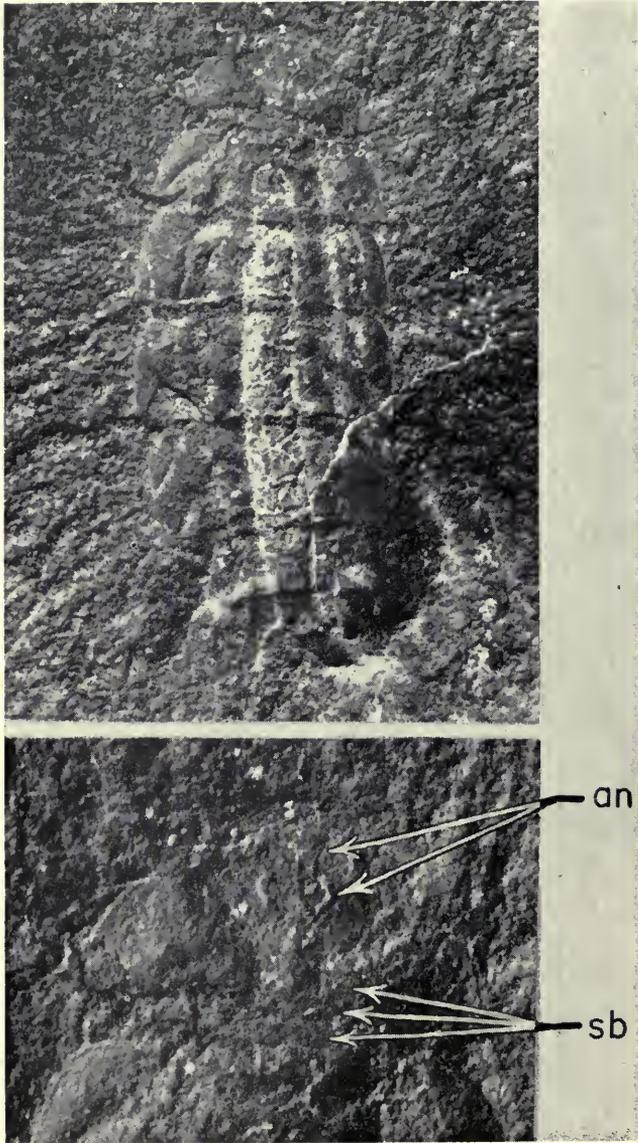


FIG. 3. *Kottixerxes gloriosus*. H122, bottom picture is a closeup of the head region with the antennae? (an) and the visible segmental borders of the cephalon (sb) marked. Top, $\times 4$; bottom, $\times 7$.

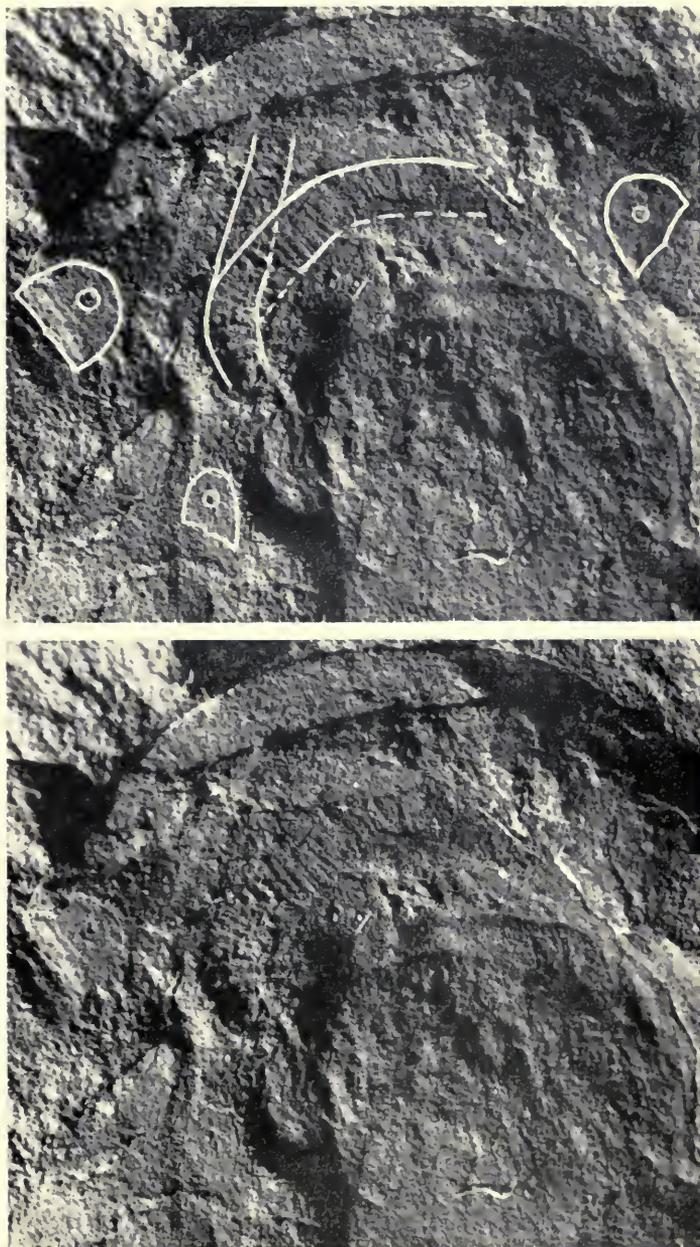


FIG. 4. *Kottixerxes gloriosus*. H410. In the upper picture, the remnants of the cephalic appendages are outlined for ease in interpreting the lower picture. Note the multisegmented rami of the "first antennae," the basal segment of the "second antennae," and the basal segment of a left "circumoral appendage." $\times 9$.



FIG. 5. *Kottixerxes gloriosus*. H409, closeup of a preabdominal appendage. $\times 10$.

posed of two segments, the third and fourth plates of three segments, and the last plate of only one segment. These thoracic plates extend laterad and ventrad from the dorsal roof of the somite, enveloping the sides of the preabdomen.

The five segments of the postabdomen are not fused together in any way. They bear no ornament and are successively reduced in width posteriorly. The postabdomen terminates in a relatively short telson, seen on only one of the specimens at hand (H406, fig. 2). (The telson is not typically preserved. It is frequently not included within the material of the concretion.)

Two small pairs of processes have been observed (H122, fig. 3; H407). It is possible they are parts of the antennae; however, they are poorly preserved in the specimens at hand and cannot be identi-

fied with any degree of certainty. There is only the vaguest suggestion of the hypostome (H122, H405, H407; fig. 3) as impressions from below on the dorsal surface of the cephalon. H410 is the only specimen examined to date, poor as it is, that reveals something concerning the structure of the cephalic appendages (fig. 4). The "first antennae" appear to be multi-segmented structures with only one ramus. Only the basalmost segments of a possible "second antenna" were observed laterad to the multi-segmented rami, so no idea as to the nature or length of the flagellum could be arrived at. On the left side of the better counterpart of H410 the basal segment of a "circumoral appendage" can be seen (lateral to the region where the mouth appears to be); possibly the vaguest sug-



FIG. 6. Holotype of *Kottixerxes gloriosus*, PE11010. $\times 2$.

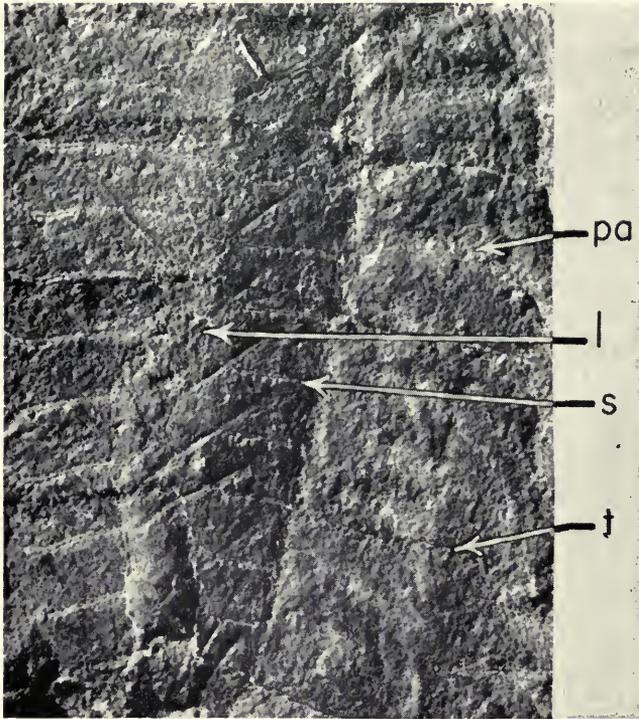


FIG. 7. *Kottixerxes gloriosus*. Closeup of T3 with the preabdominal appendages (pa), ligament (l), border of the sternites (s), and the border of the tergal plates (t) marked. $\times 6.5$.

gestion of a biramous structure in the rest of the appendage can be discerned if one examines the specimen closely.

Each of the preabdominal segments has an appendage. Appendages have been well preserved on H409 (fig. 5). Pyritic residues can be detected under xylene on H405 and ghostly outlines of the preabdominal appendages with setae can be seen on PE11010 (fig. 6) and T3 (fig. 1). It appears that the preabdominal appendages of *Kottixerxes* resemble the types described by Gall and Grauvogel (1964) for *Euthycarcinus*, *i.e.*, a single telopodite of 13 or 14 segments, each bearing setae. Heavily chitinized rod-like structures, within the body of the preabdomen, have been clearly preserved on all the specimens at hand. These structures (termed "apodemes" by Gall and Grauvogel) take origin near the anterolateral corners of the sternites and are directed at an angle posteriad and mediad (H409, fig. 5; T3, fig. 7). A small foramen is located apparently on

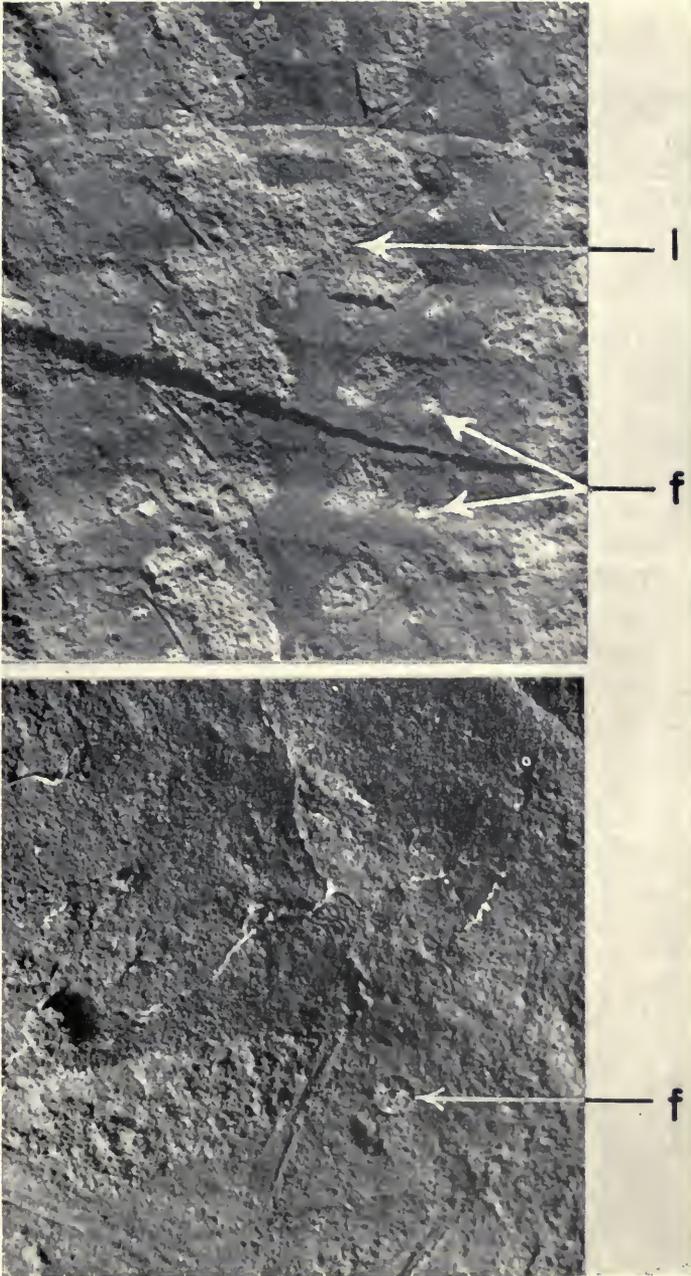


FIG. 8. *Kollixerxes gloriosus*. HTP5095, upper photo, with the ligament (l), and the accessory foramen (f). H410, lower photo. $\times 10$.

TABLE 1. Measurements in centimeters of the well-preserved specimens of *Kottixerxes gloriosus*.

	Cephalon width	Cephalon length	Pre-abdominal length	Post-abdominal length	Body length (-telson)	Telson
PE11010	1.25	.57	1.67			
PE12696	1.70		2.93			
H122	.56	.30	1.35			
H405		.70	1.83			
H406	.85	.55	1.14	.68	2.40	.36
H407	1.46	.87	2.35			
S1005		.60	1.79			
T3	1.35	.92	2.02	1.15	4.16	
T4	1.10	.75	1.98			

each segment behind the base of the appendages for that segment (HTP5095, fig. 8). There are no appendages on the postabdominal somites.

Measurements of the better preserved, available specimens are given in Table 1.

Holotype.—PE11010 (fig. 6), donated to Field Museum by A. W. Kott of Summit, Illinois.

Remarks.—The gut on almost all the specimens examined was consistently filled with very fine clastic material. These fillings, combined with the general body plan, would seem to indicate that *Kottixerxes* was a bottom-dwelling, detritus-feeding organism. This agrees with the conclusions of Gall and Grauvogel.

The rod-like structures, "apodemes," appear to have been mobile. Apodemes on opposite sides or succeeding apodemes on a side may be preserved at varying angles, which would seem to indicate that they could move. These "struts" cross segmental borders in preservation due to flattening and compression of the animal during diagenesis, but probably in life the structures were intrasegmental.

Just what the accessory foramina behind the appendages may be is a mystery. Perhaps they represent excretory pores or gonopores. They could be the openings into the telopodite; however, they appear to be too small for that.

The exoskeleton itself seems to have been only lightly sclerotized. All the specimens examined with the exception of H122 were distorted due to compression, but none were broken or cracked as would be expected if the animal were heavily armored (such as the crustacean *Belotelson magister* from this same fauna). The typically poor preservation of the preabdominal appendages indicates that even

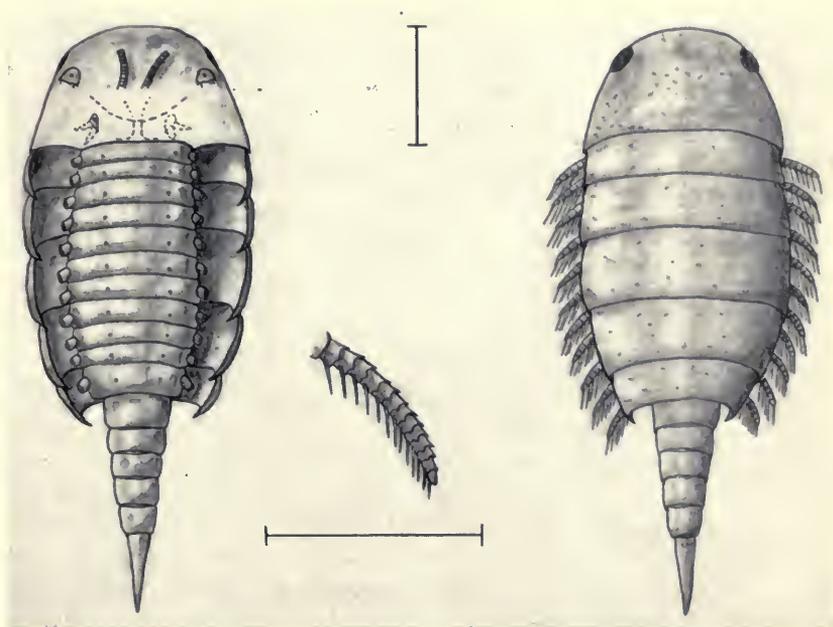


FIG. 9. Reconstruction of *Kottixerxes gloriosus*, scales 1 cm.

these structures were only lightly sclerotized. Thus we might speculate again that this animal slowly swam through the flock zone (the upper few centimeters of organically rich soup overlying the more consolidated mud) or skimmed over the surface of the sediment, feeding as it progressed.

DISCUSSION

The segmental pattern of this arthropod and the Mesozoic forms is very interesting. The preabdominal tergites are fused in groups to form preabdominal dorsal plates. In comparing the three species of euthycarcinids, (see Table 2) no pattern in the number of fused tergites per preabdominal plate emerged. Indeed, in instances where similar phenomena can be observed in the recent fauna (primarily in the "myriapod" groups) they have proven to be quite variable. All the euthycarcinids, however, have 11 (or 12) segments in the preabdomen which have fused dorsally in varying patterns into fewer plates. The postabdomen in *Euthycarcinus* has four or five segments; *Kottixerxes* has five segments, while in *Synaustrus* there are only four. The deficiency of a postabdominal segment

in *Synastrus* may be due to either a fusion of any two postabdominal segments, a fusion of the last segment with the telson, or a failure of the telson to bud off a fifth segment in this genus.

TABLE 2. Comparison of the three species of Euthycarcinidae in regard to certain aspects of their morphology. () indicates conclusions of Riek (1968).

	Pre-abdominal pattern	Post abdominal somites	Telson long	Cephalon blunted	Tergites decorated
<i>Euthycarcinus kessleri</i>	1,3,3,3,1(2)	5	+	+	+
<i>Synastrus brookvalensis</i>	1(2),2,3,3,2	4	+	-	-
<i>Kottixerxes gloriosus</i>	2,2,3,3,1	5	-	+	-

The presence of rod-like "apodemes" associated with the pre-abdominal appendages seems to be the most puzzling and controversial aspect of euthycarcinid anatomy. Riek (1964), in his original description of *Synastrus*, considered these structures to be artifacts due to preservation. He claims to be able to reproduce these by flattening any reasonably sclerotized siphonurine mayfly nymph (*personal communication*). The abdomen of these nymphs is bi-convex in section. The rod-like struts, in his experiments, represent the anterior margin of a tergite that is overlapped by the hind margin of a preceding tergite. These structures are well developed, however, on almost all specimens of *Kottixerxes*. I am inclined to agree in part with the interpretation of Gall and Grauvogel, who termed these structures "apodemes." But apodemes in modern arthropods are typically plate-like infoldings of the exoskeleton. They function as places of muscle attachment around the appendage base. These rod-like structures are very peculiar and would appear to be more like ligaments or tendons associated with the appendicular musculature or the exoskeleton. Just why these structures are developed the way they are is not clear. Why would a group of poorly sclerotized, bottom-dwelling, detritus-feeders require such specialized, apparently well-sclerotized, rod-like "ligaments" or "struts"?

There is considerable debate as to the taxonomic affinities of this group. Gall and Grauvogel, having considered the similarities of *Euthycarcinus* to the trilobitoids in passing, insisted that the euthycarcinids were true Crustacea and erected a new subclass to accommodate them. This position would seem to be unlikely when their criteria are examined. First, body regionalization is known throughout the Arthropoda and the segmentation of the regions in the euthycarcinids bears little resemblance to that in any known crustacean group. Second, two sets of antennae are not restricted

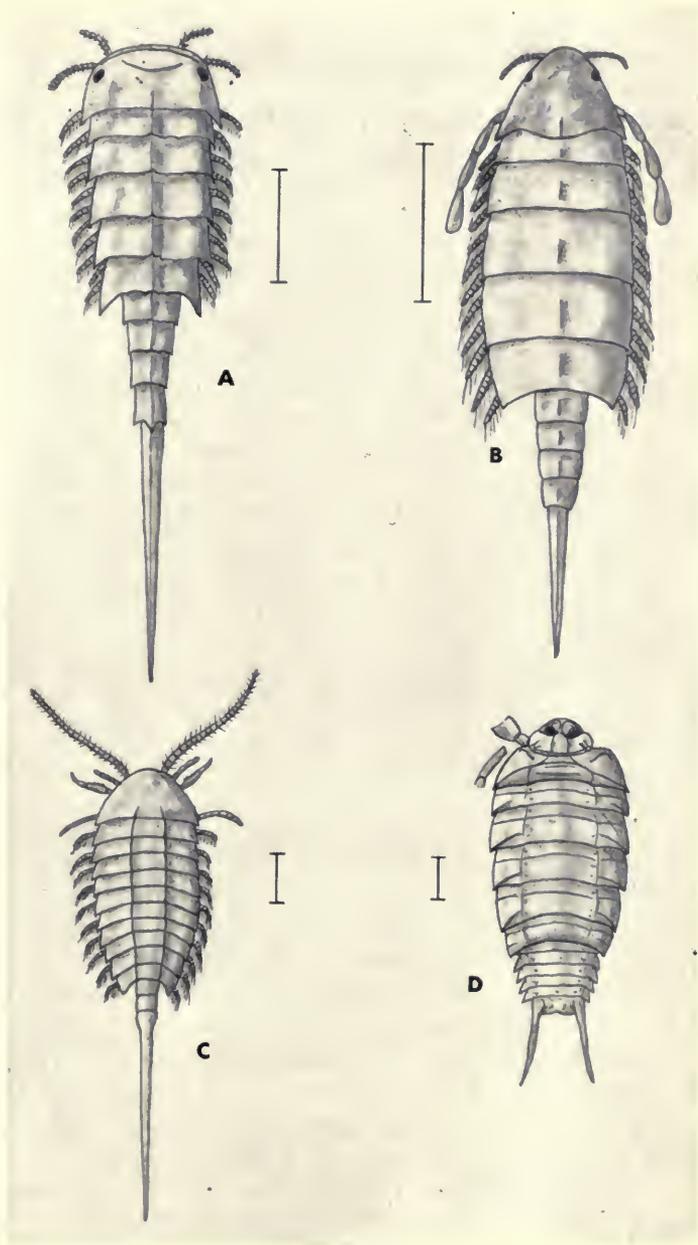


FIG. 10. A. *Euthycarcinus kessleri* (redrawn from Gall and Grauvogel, 1964); B. *Synaustus brookvalensis* (redrawn from Riek, 1968); C. *Emeraldella brooki* (redrawn from Störmer 1959); D. *Oxyuropoda ligioides* (redrawn from Carpenter and Swain, 1908). Scales 1 cm.

to the Crustacea, but occur also in some of the trilobitoids, and as such can be considered only convergent to the crustacean condition. Finally, the nature of the "mandibles" and postoral appendages is extremely obscure in all three species of euthycarcinids and cannot be safely used at this time as indicators of phyletic relationship. Furthermore, the work of Manton (1964) indicates that "mandibles" arose more than once within the living arthropods. It is possible that they also arose independently in the Euthycarcinoidea.

Riek (1968) has re-examined *Synastrus* and reinterpreted *Euthycarcinus*. He has come to agree with Gall and Grauvogel and places the Euthycarcinoidea in the Branchiopoda as a separate subclass. His reinterpretation of the cephalon would be a strong argument for this assignment, but again, the evidence is *very* inconclusive. Riek's new observations are attractive, however, and perhaps should not be rejected until all specimens of all three species can be examined. Riek (1964) originally believed *Synastrus* to be a merostomoidean. I tend to concur with this judgment. Not only is the general body plan of the euthycarcinids merestomoid, but what is known of the preabdominal appendages of all three species would indicate that this group should probably be placed in the trilobitoids. The preabdominal appendages are single-branched telopodites with 13 or 14 setiferous segments. This is more reminiscent of the condition found in some of the trilobitoids than in the Crustacea. The primitive crustacean limb, as exemplified by the cephalocarids, branchiopods, and leptostracans, apparently was a foliaceous appendage with exopods, endopods, and well-developed epipodites. The only crustacean limb that even closely approximates that found in the three euthycarcinid species is the specialized type possessed by the eumalocostraca, but even this retains the basic biramous plan. Thus I would choose to place the Euthycarcinoidea in the Merostomoidea for the present.

It is also possible that the euthycarcinoids are Merostomata. Such a designation would be more attractive than placing them in the Crustacea. Positive evidence on the nature and arrangement of the cephalic appendages would settle the question, but such is lacking. No chelicerae are indicated on any of the euthycarcinids but this is negative evidence. The possibility of assignment to the Merostomata should remain open.

Of all the Merostomoidea, the Euthycarcinoidea appear to be near the order Emeraldellida (*Emeraldella brocki* and *Molaria spinifera* Walcott, 1912). In comparing the merostomoidean orders

TABLE 3. Summary classification of the Merostomoidea with emphasis on the Euthycarinoidea.

- Subclass: Merostomoidea, Størmer, 1944
 Order: Limulavida, Walcott, 1911
 Order: Nectaspida, Walcott, 1912
 Order: Leancoiliida, Størmer, 1944
 Order: Emeraldellida, Størmer, 1944
 Order: Euthycarinoidea, Gall and Grauvogel, 1964 (*emend.* Schram, herein).
 Family: Euthycarcinidae, Handlirsch, 1914
 Euthycarcinus kessleri, Handlirsch, 1914
 Synastrus brookvalensis, Riek, 1964
 Kottixerxes gloriosus, nov.
 ?Family: Oxyuropodidae, Carpenter and Swain, 1908
 Oxyuropoda ligioides, Carpenter and Swain, 1908

with each other it appears that the differences between the euthycarcinids and the other groups merit an ordinal distinction within the framework of our current understanding of the Trilobitoidea.

It is possible that a problematic arthropod from the Devonian should be included in the Euthycarinoidea. *Oxyuropoda ligioides* Carpenter and Swain, 1908, shares a number of features with the euthycarcinid species. *Oxyuropoda* has three body regions: a cephalon, a preabdomen with five (or six) dorsal plates and the possibility of many more ventral segments, and a postabdomen of five segments with a telson bearing two rami. What Carpenter and Swain refer to as a chelate first thoracic appendage could possibly be a development of one of the antennae. From their reconstruction and description, it appears that at least their first, and possibly their second thoracic segment is actually part of the cephalon. A re-examination of the original material of *Oxyuropoda ligioides* is necessary before any definitive judgment can be made; however, it would appear that this problematic fossil might be included within the Euthycarinoidea as a separate family. Rolfe (1969) prefers to retain *Oxyuropoda* in the Tanaidacea for the time being.

The Euthycarinoidea would have a geologic range (Middle Pennsylvanian to Middle Triassic) long after the trilobitoids were thought to be extinct. The Merostomoidea were previously known only from the Middle Cambrian in the Burgess Shale of British Columbia. The latest reported supposed trilobitoid previous to Riek's observations was the Early Devonian *Cheloniellon calmani* Broili, 1933. It would appear that the trilobitoids had a very long history and underwent a rather extensive radiation, though most of their career took place in environments where they were not

preserved. The Euthycarcinoidea also cross over the Permo-Triassic boundary in which some massive extinctions of Paleozoic creatures took place. The order Euthycarcinoidea thus becomes another on a growing list of groups which cross the Permo-Triassic boundary unaffected. The study of the Essex fauna continues to reveal that the Paleozoic radiation did not suddenly come to an end, but was part of a continuum leading into the Mesozoic.

SUMMARY

A new merostomoidean trilobitoid, *Kottixerxes gloriosus*, is described. It is found to have definite affinities with two Triassic forms which together with it are placed as an order within the Merostomoidea. The presence of this order in the Late Paleozoic and Early Mesozoic indicates a long and divergent history for the trilobitoids. The known distribution of the order embraces North America, Europe, and Australia.

ACKNOWLEDGMENTS

The author wishes to acknowledge the generous co-operation he received from Messrs. Herdina, Sherman, and Tully, and Mrs. Helen Piecko. Deep thanks are extended to Mr. Kott for donating the holotype. The stimulating discussion and constructive criticism of the manuscript by Dr. E. S. Richardson, Jr. of Field Museum was, as always, perceptive and helpful, and deeply appreciated. The debate with Edgar Riek, when he was in Chicago in 1969, over interpretations of euthycarcinoidean anatomy was most stimulating. Henry Dybas of Field Museum provided discussion and analysis of modern arthropod anatomy. Thanks are also expressed to Drs. H. B. Whittington and W. D. I. Rolfe for reviewing the manuscript and suggesting modifications. However, this does not imply agreement with the author's ideas, nor in any way mitigate any defects of presentation.

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ADDENDUM

Since this paper went to press, another specimen of *Kottixerxes gloriosus* has come to the author's attention; W654 (fig. 11) from the collection of Mr. and Mrs. Fran Wolff of Park Forest, Illinois. The specimen is 14 mm. long and is composed of a cephalon, a preabdomen of 11 segments, and a postabdomen with the three proximalmost segments preserved. No appendages are detectable.

The preabdomen of this individual is distinctive. The specimen clearly displays the 11 sternites of the body trunk and the lateral extensions of 11 tergites. The tergites are not fused as they are in the adults. This specimen would seem to represent a juvenile. This small individual with unfused tergites would be from a stage in the life history of the species prior to a molt or molts which led to the fused tergal condition in the mature forms.



FIG. 11. *Kottixerxes gloriosus*, W654. Supposed juvenile form with unfused preabdominal tergites. $\times 8$.

The existence of this juvenile stage of *Kottixerxes* tends to strengthen the relationship of the Euthycarinoidea to the Cambrian merostomoideans, such as *Emeradella*, which it resembles.

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